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Catchment properties and the photosynthetic trait composition of freshwater plant communities

Short title: Catchments rule aquatic plant traits

One sentence summary: The geographical distribution of bicarbonate use in freshwater plants is controlled by catchment characteristics.

Author list:

Iversen^{*}, L. L.^{1,2}, Winkel^{*}, A.¹, Baastrup-Spohr^{*}, L.¹, Hinke, A. B.¹, Alahuhta, J.³, Baattrup-Pedersen, A.⁴, Birk, S.⁵, Brodersen, P.¹, Chambers, P. A.⁶, Ecke, F.⁷, Feldmann, T.⁸, Gebler, D.⁹, Heino, J.¹⁰, Jespersen, T. S.¹, Moe, S. J.¹¹, Riis, T.³, Sass, L.¹², Vestergaard, O.¹³, Maberly^{#§}, S. C.¹⁴, Sand-Jensen^{#§}, K.¹, Pedersen^{#§}, O.^{1, 15}

^{*} contributed equally

[§] contributed equally

[#] Corresponding author (s)

1 University of Copenhagen; 2 Arizona State University; 3 University of Oulu; 4 Aarhus University; 5 Universität Duisburg Essen; 6 Environment Canada; 7 Swedish University of Agricultural Sciences; 8 Estonian University of Life Sciences; 9 Poznań University of Life Sciences; 10 Finnish Environment Institute; 11 Norwegian Institute for Water Research; 12 University of Illinois; 13 United Nations Environmental Program; 14 Centre for Ecology & Hydrology; 15 School of Agriculture and Environment, The University of Western Australia

ABSTRACT

Unlike land plants, photosynthesis in many aquatic plants relies on bicarbonate in addition to CO₂ to compensate for the low diffusivity and potential depletion of CO₂ in water. Concentrations of bicarbonate and CO₂ vary greatly with catchment geology. Here we investigate whether there is a link between these concentrations and the frequency of freshwater plants possessing the bicarbonate use trait. We show, globally, that the frequency of plant species with this trait increases with bicarbonate concentration. Regionally however, the frequency of bicarbonate use is reduced at sites where the CO₂ concentration is substantially above air-equilibrium consistent with this trait being an adaptation to carbon limitation. Future anthropogenic changes of bicarbonate and CO₂ concentration may alter the species composition of freshwater plant communities.

MAIN TEXT

The biogeography of terrestrial plants is influenced by climatic factors; primarily air temperature and precipitation (1). Furthermore, the distribution of biochemical traits such as the two terrestrial CO₂ concentrating mechanisms, C₄ photosynthesis and Crassulacean Acid Metabolism, are linked to temperature and water availability (2). Although freshwater angiosperms evolved from terrestrial ancestors (3), their growth is controlled by light, nutrients and inorganic carbon (4) rather than water, and therefore the factors influencing their biogeography is likely to be different. Inorganic carbon potentially limits photosynthesis in aquatic systems, because the diffusion of CO₂ is 10⁴-fold lower in water than in air. Consequently, the CO₂ concentration needed to saturate photosynthesis is up to 12 times the air

equilibrium concentration (5). Moreover, rapid photosynthesis can reduce CO₂ in water substantially below air saturation (4).

In response to carbon limitation, a few aquatic angiosperms evolved the same CO₂ concentrating mechanisms found in their terrestrial ancestors, but the most frequent mechanism, found in about half of studied submerged freshwater plants, is the exploitation of bicarbonate (HCO₃⁻; (4,6)), derived from mineral weathering of soils and rocks in the catchment. Bicarbonate is the dominant form of inorganic carbon in fresh waters when pH is between ~6.3 and ~10.2, and its concentration often exceeds that of CO₂ by 10- to 100-fold (6). The ability to use bicarbonate is present in most taxonomic groups and appears to have evolved independently in cyanobacteria, eukaryotic algae and vascular aquatic plants (7). This shows the fundamental importance of bicarbonate use to plant fitness (6); increase of photosynthesis, growth and primary productivity at higher bicarbonate concentrations has been documented (8-10). However, bicarbonate use is not ubiquitous, because it involves costs as well as benefits. Costs include energy since it is an active process (11) and rates of photosynthesis at limiting concentrations of inorganic carbon are greater in CO₂ users than in bicarbonate users (5,12). Thus, where CO₂ concentrations are substantially above air saturation, as is often the case in streams, the benefit of bicarbonate use will be reduced (13). Furthermore, obligate CO₂ users can exploit alternative CO₂ sources in the air, lake sediment or in the water overlying the sediment (14), allowing continued photosynthesis without the need to invest in mechanisms required for bicarbonate use.

We hypothesized that since limitation of photosynthesis by inorganic carbon supply is widespread in freshwater plants, the relative concentration of bicarbonate and CO₂ at a particular

site should determine the proportion of plants that are obligate CO₂ users vs bicarbonate users. Since geochemical catchment characteristics determine bicarbonate concentration, there should be broad biogeographical patterns in the proportion of freshwater plants able to use bicarbonate while at a smaller scale, both the CO₂ and bicarbonate concentrations in lakes and streams might structure the functional group composition.

To test these hypotheses, we generated a database of freshwater angiosperms and their ability to use bicarbonate as an inorganic carbon source, based on data found in the literature. These were complemented with new data we gathered on 35 species from mainly tropical regions where few prior data existed (Table S1 and (15)). The resulting 131 species represent approximately 10% of known species with a submerged life stage (16) and of these, 58 (44%) could use bicarbonate. In order to quantify the distribution of bicarbonate users vs CO₂ users, we used: i) approximately 1 million geo-referenced plant records; ii) global plant ecoregion species lists; and iii) 963 site specific plant compositions from northern hemisphere lakes and streams (Fig. S1). In each of the investigated 963 sites, plant composition was related to measured concentration of CO₂ and bicarbonate. The geo-referenced plant records and ecoregion species lists were linked to local bicarbonate concentrations derived from a constructed global map of bicarbonate concentration (Fig. S2 and (15)).

In the analyzed lake and stream sites, concentrations of both bicarbonate and CO₂ affected the occurrence of obligate CO₂ users vs bicarbonate users, but differently within and between lakes and streams (Fig. 1, and Fig. S3). The chance of observing a bicarbonate user in lakes and streams correlated directly with concentrations of bicarbonate and CO₂ ($\Delta\text{Habitat} = -0.82 [-1.64;$

0.01] (mean [95% confidence intervals]; Δ represents the difference between streams and lakes in parameter estimates at the log(odds) scale, Fig S3)), Fig. 1A). However, with increasing bicarbonate concentrations, the likelihood of observing a bicarbonate user increased in lakes, but not in streams ($\Delta\beta_{\text{Bicarbonate}} = -0.82 [-1.10; -0.54]$ Fig. 1B; see (15) for an explanation of β). Moreover, with an increase in CO_2 , the chance of observing a bicarbonate user decreased in both habitat types ($\Delta\beta_{\text{CO}_2} = -0.04 [-0.22; 0.13]$, Fig. 1C). The present study shows that the concentration of bicarbonate has a different effect on the proportion of bicarbonate users in lakes vs streams. Unlike in lakes, no relationship between bicarbonate availability and bicarbonate users was found in streams. This upholds our hypothesis that where concentrations of CO_2 are high, the competitive advantage of using bicarbonate as a carbon source for photosynthesis will be reduced even if bicarbonate is available.

Across global plant regions (17), the shifting proportions of bicarbonate users vs obligate CO_2 users showed distinct spatial patterns (Fig. 2A). Compared to the overall mean, a higher proportion of bicarbonate users was observed in Africa, temperate Asia, and the northern part of North America (Fig. 2A). Globally, species utilizing bicarbonate were found in areas with higher bicarbonate concentrations (bicarbonate users - CO_2 users = $0.16 [0.02; 0.30]$ mM; Fig. 2C; see Fig. 3 for a local example). The proportion of bicarbonate using species increased with bicarbonate concentrations within ecoregions ($\beta = 0.14 [0.05; 0.24]$, (mean [95% confidence limits]), Fig. 2B). Because catchment geology and geological history shape the distribution of lakes and rivers, as well as the bicarbonate concentrations in freshwater ecosystems (18,19), they are the chief determinants of plant distribution in freshwaters. CO_2 concentrations are largely regulated by local CO_2 supersaturated inflow (20) and ecosystem metabolism, making modeling

difficult at large spatial scales (19,21). Thus, future models of freshwater CO₂ concentrations may improve the prediction of plant distributions even further. Although global lake and river data exist to some extent as annual means (22), given the temporal variability in CO₂ concentration, the appropriate concentration would be that during the growing season at the specific site (20).

Anthropogenic changes as a consequence of deforestation, cultivation of land, application of nitrate fertilizers and reduced atmospheric acid deposition (23) are causing large scale increases in bicarbonate concentrations (24,25). The observed increasing bicarbonate concentrations are expected to cause a severe impact on bicarbonate poor lakes, because higher bicarbonate concentrations will markedly change species composition (26) by allowing tall, fast growing bicarbonate users to colonize and suppress smaller species adapted to the use of CO₂ alone in or near the sediment (27). There is evidence for re-establishment of species that are able to use bicarbonate, after bicarbonate has increased because of liming (28) or as a result of reduction in acid deposition (29). Moreover, systematic changes in species composition caused by changes in CO₂ concentration has also been demonstrated in a river system where the proportion of CO₂ users declined as CO₂ decreased downstream (13). In contrast, increasing atmospheric CO₂ concentrations, even if they influence dissolved CO₂, will have little effect on the abundance of bicarbonate users, since increases in CO₂ will be small relative to bicarbonate concentrations and will have little effect on plant photosynthesis rate (30).

Our study shows that bicarbonate use by aquatic angiosperms is widespread in fresh waters around the globe, and that the proportion of obligate CO₂ users to bicarbonate users is

significantly related to the bicarbonate concentration. Among terrestrial plants, the evolution of leaf traits and different photosynthetic pathways that enable rapid carbon assimilation and improved water economy (31) has resulted in global biogeographical patterns that are linked to variations in climate (32,33). In contrast, for freshwater plants, we show that biogeographical patterns of bicarbonate use exist and that these are caused by catchment properties that determine the concentration of bicarbonate and CO₂. This insight will help evaluate the repercussions of future changes in concentration of bicarbonate and CO₂ on the biodiversity and ecosystem function for fresh waters.(34)

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242

243 **Competing interests:** The authors declare no competing interests.

244

245 **Data availability:** All R scripts and cleaned datasets used for this analysis are available at the

246 Dryad Digital Repository.

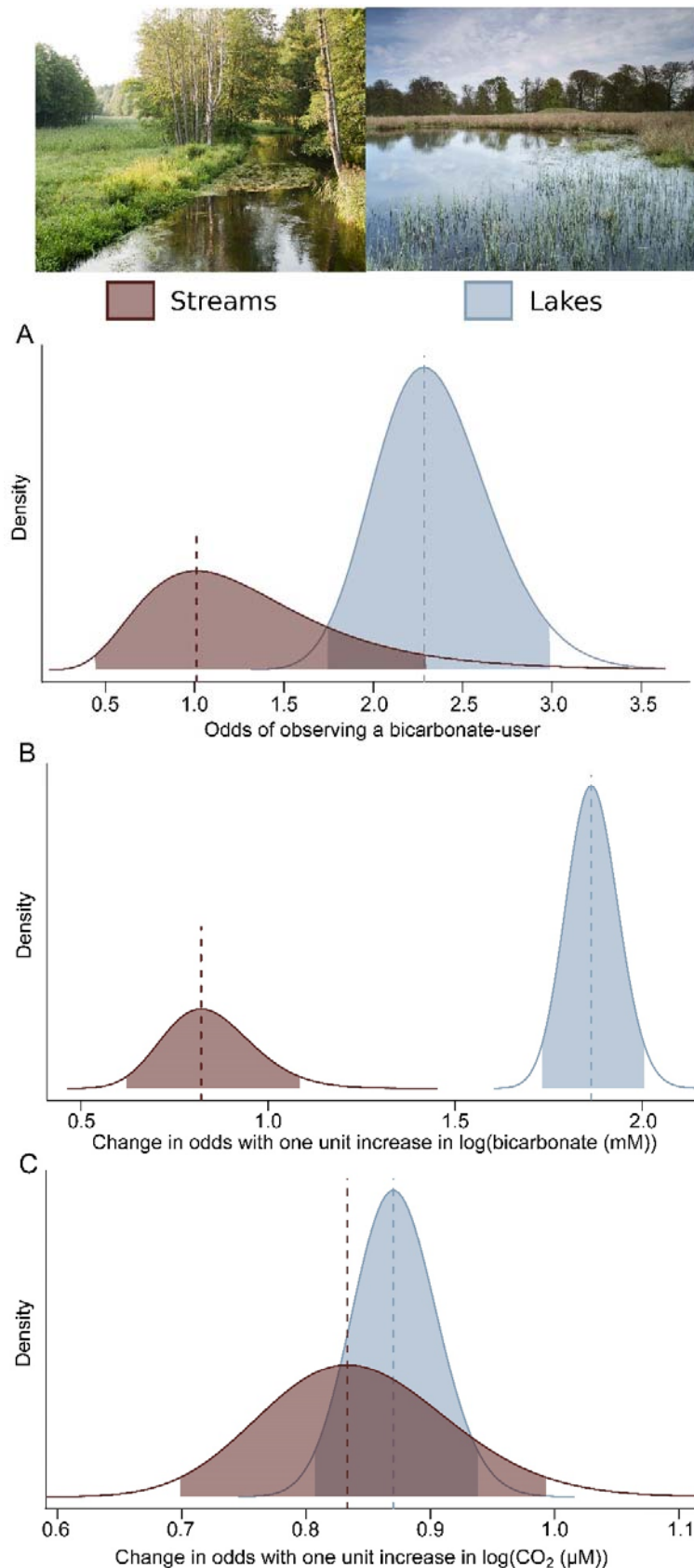


Fig. 1

Bicarbonate use in submerged freshwater plant communities.

(A) likelihood of observing a bicarbonate user vs a CO₂ user in streams (n=172, red) and lakes (n=791, blue); (B and C), modeled odds of observing a bicarbonate user vs a CO₂ user as a function of bicarbonate (B) and CO₂ (C) concentrations. Values > 1 indicate a higher likelihood (A) or increase in likelihood (B and C) of observing a bicarbonate user vs a CO₂ user with a one unit increase in bicarbonate (B) and CO₂ concentrations (C). The dotted vertical lines show mean estimates and shaded areas the 95% confidence limits around the mean.

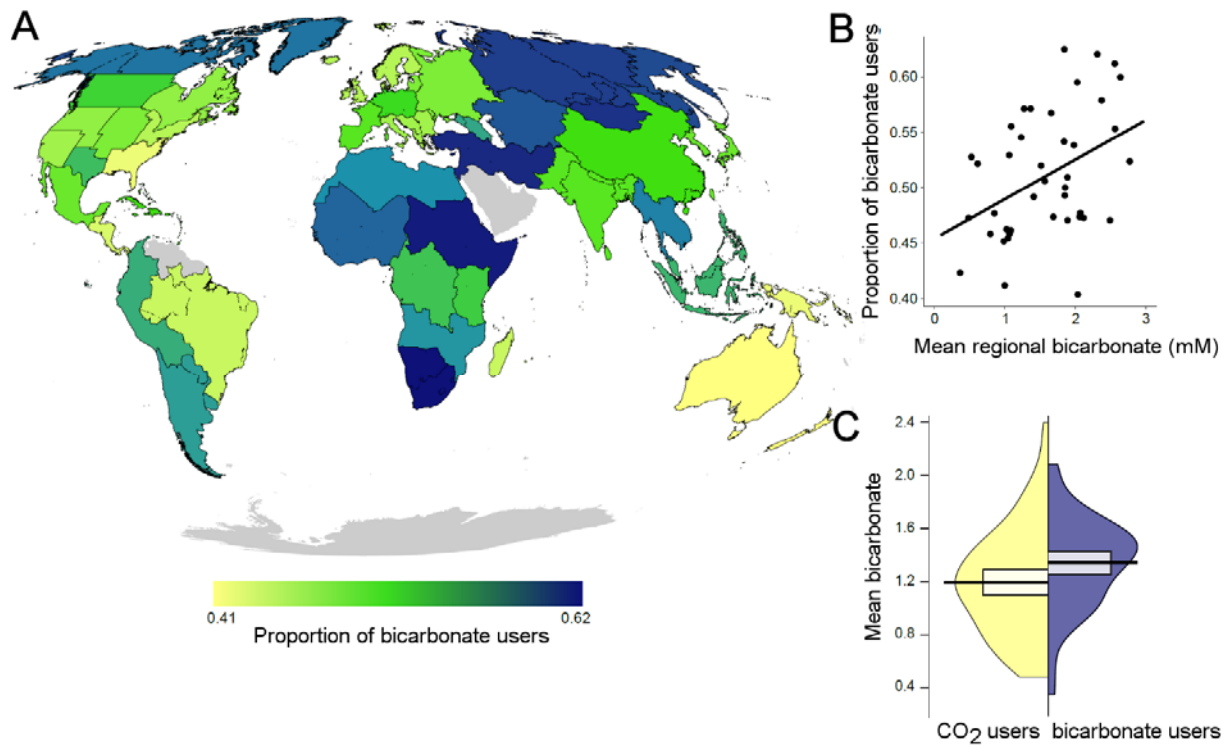


Fig. 2

Global relationship between bicarbonate and the proportion of bicarbonate users in freshwater plants. (A) Proportion of bicarbonate using species across 52 plant ecoregions. Grey areas indicate regions where information on bicarbonate use in local plants is not available. (B) Relationship between mean bicarbonate concentration in plant regions and frequency of bicarbonate users. The line represents the mean proportion of bicarbonate users. (C) Density plots of bicarbonate preferences for bicarbonate users ($n = 57$) and obligate CO_2 users ($n = 72$). The central horizontal black line represents the mean and the boxes indicate the 95% confidence intervals around the mean.

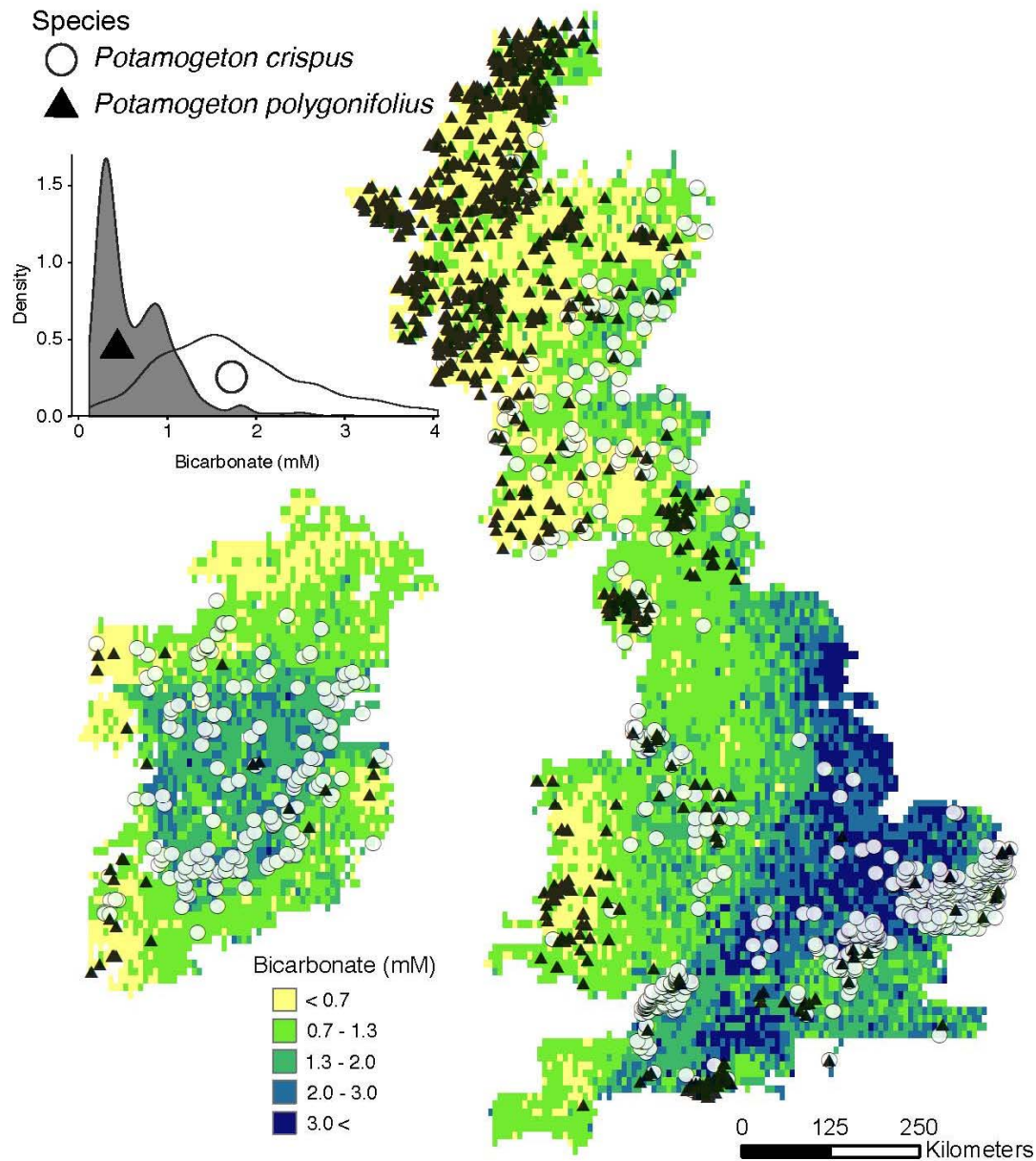


Fig. 3

Steep gradients in bicarbonate concentrations and spatial separation in species distribution in the British Isles. Distribution of two pondweed species with contrasting bicarbonate use in the British Isles. *Potamogeton polygonifolius* (obligate CO₂ user, black triangles) is found in areas with lower bicarbonate concentrations compared to *Potamogeton crispus* (bicarbonate user, white circles). The top left insert shows the density distribution of the two species across

305 bicarbonate concentrations. Bicarbonate concentrations are from the global bicarbonate map
306 (Fig. S2) and species data were extracted from the geo-referenced plant occurrences (15).

307

308 **Supplementary Materials**

309 Materials and Methods (15).

310 References (34-90).

311 Fig. S1 - Site-specific observations of bicarbonate use.

312 Fig. S2 - Global bicarbonate map.

313 Fig. S3 - The probability of observing bicarbonate use in a species at 963 study sites.

314 Fig. S4 - Overview of *in situ* lake bicarbonate measurements.

315 Fig. S5 - Variable importance plot of the Random Forest modelling global bicarbonate
316 concentrations.

317 Fig. S6 - Partial dependence plots of the eight variables used to model global bicarbonate
318 concentrations.

319 Fig. S7 - Histogram of taxonomic distinctness for 1000 random subsamples of a fixed number of
320 131 species drawn from a common species pool.

321 Table S1 - List of freshwater angiosperms and their trait of inorganic carbon use.